

10

Identifying Units to Conserve

HREE HUMAN GENERATIONS AGO, MY great-grandparents paused in their westward move while herds of migrating buffalo crossed the Missouri River in front of their steamboat. Long before the birth of my father, the migratory herds of the North American Great Plains were a distant memory, and the plains ecosystems had been forever changed. Similar hunting zeal resulted in the near-extermination of the great migrating "herds" of whales in my lifetime. We humans now choose what we will conserve into the future. We choose whether the blue whale species will be represented by multiple healthy populations throughout its former range or by a single remnant population. The question of how to define "units to conserve" is not a question of how to define a species, but rather how to define a vision of the future.

In the United States our vision for natural resource management is implemented through various treaties, laws, and regulations in which we assume that discrete conservation units can be delineated from animal and plant populations that are by their nature continuous. Where do we draw the line? By analogy, where do we draw the line in saying that someone is "family"? It is easy to say that your sibling or parent is family, but what about a second cousin or someone who shares the same last name but comes from a different country? Drawing the categorical boundaries is often difficult even though we recognize that we are members of a hierarchy of relatedness ranging from immediate family to our racial makeup to being a human and even to being a primate and a mammal. Generally, as distance within the hierarchy increases, it is increasingly easy to place the categorical boundary unambiguously. For example,

telling a vertebrate from an invertebrate is simple, whereas telling human races apart genetically is not. From an evolutionary perspective, the strength of the categorical boundary increases with the depth of the evolutionary branch in the tree of life.

Management of animals and plants usually occurs at or below the species level. Scientists still have some difficulty defining and identifying species, more difficulty at the subspecies level, and much more at yet lower levels. Despite the difficulties of defining units at lower levels, properly categorizing units is necessary if we want to be able to implement our vision of the future and reach our objectives. Success depends on three steps: (1) defining "units" that match ideals, which is largely a policy/societal choice; (2) identifying the units in nature, which is a scientific undertaking; and (3) making necessary management decisions and taking action as needed. Although these steps seem discrete, there is a good deal of necessary iteration among them to get the full process operating effectively. Nonetheless, scientific identification of appropriate conservation units is essential for achievin g society's long-term objectives and vision. For example, and as described later in this chapter, failure to recognize the southern resident population of killer whales off the U.S. West Coast as a distinct population segment likely would have reduced management efforts to bring about its recovery and increased its chance of extinction. Although I am concerned primarily with the science of identifying such units, I begin by reviewing the existing hierarchy of units to conserve both in the United States and at international levels for marine mammals.

Both U.S. and international laws and treaties have been influenced by past excessive human exploitation of marine mammals. Eight of the species originally listed under the U.S. Endangered Species Act (ESA) were large whales. Despite decades of protection, many parts of the ocean remain devoid of certain whale species. Thus, even though the oceans

may appear to us to have no barriers to movement, the animals that live there do perceive barriers. In fact, recent research using photographic identification, branding, radio and satellite-tagging, and genetic methods have indicated that most marine mammals have a very distinct population structure, which may be most evident in their patterns of movement. Some, like humpback whales, appear not dissimilar to migratory herds of caribou with distinct summering and wintering grounds to which they return faithfully. Others, like harbor seals, roam when they are young but usually settle down as adults near their birth site. Should our vision be to maintain healthy numbers of marine mammals throughout their range, scientists and managers have to understand their population structure in order to manage human impacts such as hunting or incidental kills in fisheries. Similarly, if we want to understand the magnitude of the effects of pollutants from a particular point source on marine mammals in the vicinity, that "vicinity" must be described for different species, and it will clearly differ for resident species compared to migratory species.

Conservation science provides the tools and knowledge needed to implement society's vision of the future. A vision of maintaining a healthy ecosystem complete with top predators, such as Steller sea lions, killer whales, and sea otters, requires using science to understand how these populations are structured. I discuss three hierarchical levels of structural units: (1) species, (2) subspecies and distinct population segments (DPSs), and (3) stocks (Fig. 10.1). The scientific literature uses many terms to refer to different levels of structure, and I briefly review these and how they fit into the three levels discussed here. I refer to all the terms that embody structure at different levels as "units to conserve" (UTCs). All these levels have been deemed worthy of conservation in different national and international laws although some laws, such as the ESA, focus on conservation primarily at the species and subspecies levels. All these terms are

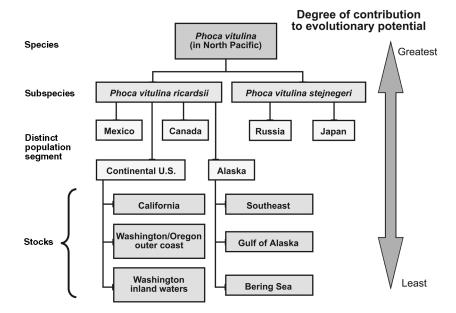


Fig. 10.1. Hypothetical schematic of the hierarchical relationships of different units to conserve, using harbor seals as an example. As DPSs have not been defined for harbor seals, this example is hypothetical and draws DPS boundaries solely according to the criterion of national boundaries. The stocks shown are those in 2003 stock assessment reports. For simplicity, only the North Pacific is shown.

explained in detail later in the chapter, but, briefly, units at the species and subspecies levels are on different evolutionary trajectories and therefore represent important evolutionary potential. Stocks are units whose population dynamics are essentially independent of neighboring stocks (called demographically independent) but *may or may not* represent important evolutionary potential. Thus, units shown in the hierarchy in Figure 10.1 are ordered from greatest (species) to least (stocks) in terms of the contribution they make to evolutionary potential.

The purpose of this chapter is to review conservation unit concepts, consider how these concepts pertain to marine mammal conservation, and suggest where research focus is most needed. I illustrate concepts and problems associated with identifying UTCs with case studies on killer whales and harbor seals. These cases indicate the most important research and management needs regarding UTCs:

- Adequate recognition and treatment of the scientific uncertainties involved.
- Corresponding development and testing of analytical tools to define stocks in a probabilistic manner.
- Development of working UTC definitions that incorporate scientific uncertainty in a precautionary manner.

UNITS TO CONSERVE: SPECIES, SUBSPECIES, AND DISTINCT POPULATION SEGMENTS

Laws and treaties make an implicit assumption that scientists have already properly defined species and subspecies. For example, the ESA defines species [Section 3(15)] as "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." Similarly, the Convention on the International Trade of Endangered Species of Wild Fauna and Flora (CITES) and the Red List, developed by IUCN-TheWorld Conservation Union, assume accurate definitions. Clearly, mistakes in implementing these laws and treaties are likely if species and subspecies remain unidentified. Nevertheless, scientists are still identifying new species and subspecies of cetaceans, including large whales. For example, northern right whales, listed in the original ESA, have recently been split into two species, North Atlantic right whales and North Pacific right whales (Rosenbaum et al. 2000), based on genetic data. This departs from previous general practice in taxonomy (the naming of species and subspecies), which has used primarily morphology, especially skull measurements, to designate species.

Designation of a species without corroborating morphological data, as for the right whale case, remains controversial among taxonomists. This instance demonstrates why traditional taxonomy lags behind and may not be appropriate for species designations involving marine mammals: adequate skull collections are not, and often will not become, available. To promote more timely progress in

cetacean taxonomy, a workshop was held in April 2004 to develop and agree on new definitions and criteria for species and subspecies (Reeves et al. 2004). Workshop participants agreed that (1) multiple species concepts should be acknowledged; (2) two congruent lines of evidence should be required to define a species, which would ideally incorporate both morphological and genetic data but could be based on two independent genetic markers; (3) only a single line of appropriate evidence should be required to define a subspecies and this may be a genetic marker; and (4) subspecies could be either a geographic form or an incipient species. Because they validate the use of genetic data in taxonomic designations, these guidelines pave the way for more timely resolution of taxonomic uncertainty in many marine species for which substantial skull morphometric datasets are unlikely to be obtained in the foreseeable future.

Species (excerpted from Reeves et al. 2004)

Definition: The workshop acknowledged that both major species concepts—the Biological Species Concept (BSC) and the Phylogenetic Species Concept (PSC), as well as their various subapproaches—have merit and should be considered relevant and useful in cetacean taxonomy. It was agreed that the different approaches to species delimitation should be employed in a flexible and pragmatic way, with the basic aim of using proxies to identify irreversible divergence. Multiple lines of evidence are essential, and what ultimately matters is that a convincing argument is provided demonstrating irreversible divergence.

Criteria: Both morphological data and genetic data can be taken as proxies for reproductive isolation and irreversible divergence. It is possible, however, for individual morphological characters to be convergent and for the data from one genetic locus not to reflect phylogenetic history because of homoplasy or natural selection. Therefore, a finding of congruent divergence for each of multiple distinct kinds of data should be taken as strong support for species designations. Such distinct kinds of data could include morphological data together with genetic data or data from multiple independent genetic loci. In the case of morphological data, any phenotypic character is acceptable. Ideal datasets, including both morphological data and data from multiple loci, can provide not only a large amount of information for decisions regarding species, but also the information necessary to assess the uncertainty associated with that decision.

Data on geographical ranges and on behavior (e.g., feeding behavior and vocalizations) can complement morphological and genetic data and serve as useful lines of evidence in species delimitation. Given the difficulties of knowing the degree to which geographical distribution and behavior actually reflect genetic divergence, however, these kinds of data should not be the primary basis of such delimitation.

¹ Although hybridization does occur in cetaceans, these rare events do not lead to separate species merging to become one and hence are consistent with the term irreversible divergence.

Subspecies (excerpted from Reeves et al. 2004)

Definition: A critical distinction between species and subspecies involves the question of reticulation,² or reversibility. In the case of a subspecies, it may not be possible to demonstrate that the population is on an independent evolutionary trajectory without reticulation, while such demonstration is a requirement for species status. Because subspecies (and ESUs³) are on a continuum, it should be no surprise that distinctions are often problematic and require judgments by the investigator as to the strength of a given factor or suite of factors. Thus, the subspecies concept may be construed as broad enough to contain two types of entities: (1) populations that are not quite far enough along the continuum to be judged as species, and (2) populations that should be species but for which not quite enough evidence is yet available to justify their designation as such.

Thus far, cetacean subspecies have been geographical forms that are noticeably different. Therefore, designations have been based on a combination of morphology and distribution. In the context of this workshop, attention was drawn to the potential for bringing genetic evidence, including neutral markers, into the subspecies definition. It was suggested that for many cetacean species, the difficulty of bringing together, over a reasonable timescale, the large, representative series of osteological specimens needed for definitive morphological comparisons is effectively insurmountable. This is true, for example, for many of the elusive, offshore beaked whale species, the wide-ranging killer whales, and all of the large whales. Thus, for taxonomy at the subspecies level to be relevant for conservation, the range of evidence that can be used needs to be broadened to include genetic markers.

Criteria: In addition to the use of morphology to define subspecies, the subspecies concept should be understood to embrace groups of organisms that appear to have been on independent evolutionary trajectories (with minor continuing gene flow), as demonstrated by morphological evidence or at least one line of appropriate genetic evidence. Geographical or behavioral differences can complement morphological and genetic evidence for establishing subspecies. As such, subspecies could be geographical forms or incipient species.

Participants in the cetacean taxonomy workshop also produced a prioritized list of species for which we most need further taxonomic research (Table 10.1), based on both taxonomic uncertainty and conservation status (Table 10.2; Reeves et al. 2004). Most of the seventeen species given highest priority ranking are found in non-U.S. waters, especially coastal dolphins in and near Asia. Proper identification of species and subspecies is critical to international conservation activities such as those undertaken by the International Whaling Commission (IWC), required by the CITES, and in accordance with the Red List maintained by the IUCN. In some instances critically endangered subspecies or

even species remain unrecognized and therefore are more vulnerable to human activities. In other instances human activities may be restricted unnecessarily because of inadequate understanding of population structure.

There are actually two types of units that are below the species level but are still likely to be on a different evolutionary path: subspecies and distinct population segments (DPSs). Both units are used to conserve the essential genetic variability for future evolutionary potential. That is, conservation of both units is intended to maintain sufficient evolutionary potential that the species can respond to future environmental challenges through adaptation.. The DPSs (defined later in the chapter) are recognized as "species" in the ESA and are equivalent to the evolutionarily significant unit (ESU), an earlier designation that was used primarily for salmon (Dizon et al. 1991, Waples 1991, Moritz 1994). I use only the term DPS, which for the purposes of this discussion is the same as an ESU. The division between subspecies and DPSs is unclear given the new criteria for subspecies for cetaceans, as described previously, but it seems likely that they differ by a matter of time elapsed since separation. For subspecies, the most closely related units have been separated long enough that morphological differences may have accrued. The DPSs, in contrast, are experiencing sufficiently low gene flow that local adaptation may occur. A rule of thumb often used to distinguish DPSs, which is also used by the IUCN to define "regional populations" (Gärdenfors et al. 2001) of global species, is that the level of gene flow between or among them is less than one disperser per generation. The number of different terms used (subspecies, ESU, regional population, and DPS) can lead to confusion, but they all indicate units that are important to the evolutionary potential of the species and receive the same level of protection under the various national laws and international treaties as a full species.

Criteria to be used to designate a DPS were established in the joint agreement of the agencies charged with implementing the ESA—the U.S. Fish and Wildlife Service (FWS) and the National Marine Fisheries Service (NMFS). In the "Policy Regarding the Recognition of Distinct Vertebrate Population Segments" (U.S. Fish and Wildlife Service 1996), the FWS and NMFS concluded that DPSs should be determined based on three sequential considerations: (1) the discreteness of the population relative to the rest of the species, (2) the significance of the population segment to the species, and (3) the population segment's conservation status in relation to the ESA's standards for listing (i.e., is the population segment endangered or threatened when treated as if it were a species?).

A population segment of a vertebrate species may be considered discrete if it satisfies one of the following criteria. First, is it markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Genetic distinctness has been used as a proxy for the aforementioned factors. Or second, is the group delimited by international governmental

² In this context reticulation pertains to gene flow between two evolutionary lineages.

³ "ESUs" are evolutionarily significant units (see Dizon et al. 1991, Waples 1991, and Moritz 1994).

Table 10.1 Cetacean species and subspecies, with priority rankings for taxonomic research

pecies (common name)	Species or subspecies (Latin name)	Risk/taxonomic uncertainty	Subspecies (common name)
owhead whale—3	Balaena mysticetus	(H,L)	
Forth Atlantic right whale—3	Eubalaena glacialis	(H,L)	
North Pacific right whale –3	Eubalaena japonica	(H,L)	
outhern right whale—3	Eubalaena australis	(M,L)	
bygmy right whale—3	Caperea marginata	(L,M)	
Gray whale—3	Eschrichtius robustus		
•		(H,L)	
Blue whale—1	Balaenoptera musculus	(M,H)	C
	2	(M,M)	Common blue
	2	(M,M)	Pygmy blue whale
	1	(M,H)	Northern Indian Ocean blue whale
	2	(M,M)	Antarctic blue whale
in whale	Balaenoptera physalus		
	3	(L,M)	Northern Hemisphere fin whale
	2	(M,M)	Southern Hemisphere fin whale
ei whale	Balaenoptera borealis		
	2	(M,M)	Northern Hemisphere sei whale
	2	(M,M)	Southern Hemisphere sei whale
Common Bryde's whale—1	Balaenoptera brydei	(M,H)	
ygmy Bryde's whale—1	Balaenoptera edeni/Omurai?	(H,H)	
Common minke whale—1 or 2	Balaenoptera acutorostrata		
	3	(M,L)	North Atlantic minke whale
	1	(M,H)	North Pacific minke whale
	2	(M,M)	Dwarf-form minke whale
antarctic minke whale—3	Balaenoptera bonaerensis	(L,L)	
Humpback whale—2	Megaptera novaeangliae	(M,M)	
perm whale—3	Physeter macrocephalus	(L,L)	
rygmy sperm whale—3	Kogia breviceps	(L,M)	
Owarf sperm whale—3	Kogia sima		
Amazon River dolphin—1 or 2	Inia geoffrensis	(L,H)	
mazon River dolphin—1 of 2	2	(M M)	Amazon dolphin
		(M,M)	-
	1	(H,M)	Orinoco dolphin
	1	(H,M)	Bolivian dolphin
Gangetic dolphin—1	Platanista gangetica		
	???[AQ2]	(H,H)	Ganges dolphin
	???	(H,H)	Indus dolphin
ranciscana—2	Pontoporia blainvillei	(M,M)	
angtze River dolphin (Baiji)—3	Lipotes vexillifer	(L,H)	
saird's beaked whale—2	Berardius bairdii	(M,M)	
rnoux's beaked whale—3	Berardius arnuxii	(L,L)	
North Atlanticbottlenose whale—2	Hyperoodon ampullatus	(M,M)	
outhern bottlenose whale—3	Hyperoodon planifrons	(L,M)	
ndo-Pacific beaked whale—3	Indopacetus pacificus	(L,L)	
hepherd's beaked whale—3	Tasmacetus shepherdi	(L,L)	
Cuvier's beaked whale—1	Ziphius cavirostris	(H,M)	
lector's beaked whale—3	Mesoplodon hectori	(L,L)	
rue's beaked whale—3	Mesoplodon mirus	(L,M)	
Gervais' beaked whale—3	Mesoplodon europaeus	(L,M)	
owerby's beaked whale—3	Mesoplodon bidens	(L,L)	
Gray's beaked whale—3	Mesoplodon grayi	(L,L)	
ygmy beaked whale—3	Mesoplodon peruvianus	(M,L)	
andrews' beaked whale—3	Mesoplodon bowdoini	(L,L)	
pade-toothed whale—3	Mesoplodon traversii	(L,L)	
Iubbs' beaked whale—2	Mesoplodon carlhubbsi	(M,M)	
Sinkgo-toothed beaked whale—3	Mesoplodon ginkgodens	(L,M)	
tejneger's beaked whale—1	Mesoplodon stejnegeri	(H,M)	
ayard's beaked (Strap-toothed) whale—3	Mesoplodon layardii	(L,L)	
errin's beaked whale—3	Mesoplodon perrini	(L,L)	
slainville's beaked whale—1	Mesoplodon densirostris	(H,M)	
	Monodon monoceros	(M,M)	
Narwhal—2		(M.T.)	
Narwhal—2 Beluga or white whale—3	Delphinapterus leucas	(M,L)	
	Delphinapterus leucas Neophocaena phocaenoides	(M,L) (H,H)	
seluga or white whale—3			Indian Ocean finless porpoise
seluga or white whale—3	Neophocaena phocaenoides	(H,H)	Indian Ocean finless porpoise Western Pacific finless porpoise

Species (common name)	Species or subspecies (Latin name)	Risk/taxonomic uncertainty	Subspecies (common name)
Harbor porpoise	Phocoena phocoena		
	2	(M,M)	Black Sea harbor porpoise
	2	(M,M)	North Atlantic harbor porpoise
	2	(M,M)	Eastern North Pacific harbor porpoise
	2	(M,M)	Western North Pacific harbor porpoise
Spectacled porpoise—2	Phocoena dioptrica	(M,M)	
Vaquita—3	Phocoena sinus	(H,L)	
Burmeister's porpoise—2	Phocoena spinipinnis	(M,M)	
Dall's porpoise—2	Phocoenoides dalli	(M,M)	
Commerson's dolphin—2	Cephalorhynchus commersonii		
	2	(M,M)	South American Commerson's dolphin
old 111.	3	(L,M)	Kerguelen Commerson's dolphin
Chilean dolphin—3	Cephalorhynchus eutropia	(M,L)	
Heaviside's dolphin—3	Cephalorhynchus heavisidii	(M,L)	
Hector's dolphin—3	Cephalorhynchus hectori	(11)	C
	???	(M,L)	South Island Hector's dolphin
Shout booked common delphin 2	??? Delphinus delphis	(H,L)	North Island Hector's (Maui's) dolphin
Short-beaked common dolphin—2 Long-beaked common dolphin—2	1 1	(M,M)	
Long-beaked common dolphin—2	Delphinus capensis ???	(M,M)	Indo-Pacific common dolphin
	???	(M,M)	Long-beaked common dolphin
Pygmy killer whale—3	Feresa attenuata	(L,M)	Long-beaked common dolphin
Short-finned pilot whale—2	Globicephala macrorhynchus	(M,M)	
Long-finned pilot whale—3	Globicephala melas	(L,M)	
Long inned phot whate 3	???	(L,L)	North Atlantic long-finned pilot whale
	???	(L,M)	Southern Hemisphere long-finned pilot whale
Risso's dolphin—2	Grampus griseus	(M,M)	
Fraser's dolphin—2	Lagenodelphis hosei	(M,M)	
Atlantic white-sided dolphin—3	Lagenorhynchus acutus	(L,L)	
White-beaked dolphin—3	Lagenorhynchus albirostris	(L,L)	
Peale's dolphin—3	Lagenorhynchus australis	(L,L)	
Hourglass dolphin—3	Lagenorhynchus cruciger	(L,M)	
Pacific white-sided dolphin—2	Lagenorhynchus obliquidens	(M,M)	
Dusky dolphin—2 or 3	Lagenorhynchus obscurus		
	???	(M,M)	South American dusky dolphin
	???	(L,M)	South African dusky dolphin
	???	(L,M)	New Zealand dusky dolphin
Northern right whale dolphin—3	Lissodelphis borealis	(L,L)	
Southern right whale dolphin—3	Lissodelphis peronii	(L,M)	
Irrawaddy dolphin—1	Orcaella brevirostris	(H,H)	
Killer whale—1	Orcinus orca	(M,H)	
Melon-headed whale—2	Peponocephala electra	(M,M)	
False killer whale—2	Pseudorca crassidens	(M,M)	
Tucuxi—1	Sotalia fluviatilis	(MII)	Marine tucuxi
	??? ???	(M,H)	Freshwater tucuxi
Atlantic humpbacked dolphin—1	sousa teuszii	(M,H) (H,M)	riesiiwater tucuxi
Pacific humpbacked dolphin—1	Sousa teuszti Sousa chinensis	(H,H)	
Pantropical spotted dolphin—2	Stenella attenuata	(M,M)	
r antropicar spotted dolprini – 2	3	(M,L)	Eastern Pacific offshore spotted dolphin
	2	(M,M)	Hawaiian spotted dolphin
	3	(M,L)	Eastern Pacific coastal spotted dolphin
Clymene dolphin—3	Stenella clymene	(L,M)	of a seem and the seem and the seem and the seems are seen and the seems
Striped dolphin—2	Stenella coeruleoalba	(M,M)	
Atlantic spotted dolphin—2	Stenella frontalis	(M,M)	
Spinner dolphin—2	Stenella longirostris	(M,M)	
	????	(M,M)	Gray's spinner dolphin
	???	(M,L)	Eastern spinner dolphin
	???	(M,L)	Central American spinner dolphin
	???	(M,L)	Dwarf spinner dolphin
Rough-toothed dolphin—2	Steno bredanensis	(M,M)	
Common bottlenose dolphin—1	Tursiops truncatus	(M,H)	
Indo-Pacific bottlenose dolphin -1	Tursiops aduncus	(M,H)	

Note: Priority ranking is as follows: 1, high; 2, medium; 3, low priority (see text and Table 10.2). Species with at least one high-priority subspecies are indicated in bold. Subspecies mainly from Rice (1998).

Table 10.2 Basis for integrating taxonomic uncertainty and conservation risk in order to rank species according to the importance of taxonomic research in relation to conservation

		Taxonomic uncertainty				
		High	Medium	Low		
Conservation risk	High Medium Low	1 1 3	1 2 3	3 3 3		

Note: Priority ranking is as follows: 1, high; 2, medium; 3, low priority (see Table 10.1). Taxonomic uncertainty takes into account distributional discontinuities, especially between ocean basins.

boundaries within which there are differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms that are significant in light of Section 4(1)(1)(D) of the Act.

A population segment that satisfies at least one of the above criteria for discreteness is looked at in terms of its biological and ecological significance for the species. This consideration may include, but is not limited, to the following: (1) persistence of the discrete population segment in an ecological setting that is unusual or unique for the taxon; (2) evidence that the loss of that segment would result in a significant gap in the range of the taxon; (3) evidence that the segment represents the only surviving natural occurrence of a taxon that may be more abundant as an introduced population outside its historic range; and (4) evidence that the segment differs markedly from other populations of the species in its genetic characteristics. As circumstances are likely to vary considerably from case to case, it is not possible to describe prospectively all the classes of information that might bear on the biological and ecological importance of a discrete population segment.

Finally, if a population segment is discrete and significant (i.e., it is a distinct population segment), its evaluation for endangered or threatened status will be based on the ESA's definition of those terms and a review of the factors enumerated in Section 4(1) of the Act. It may be appropriate to assign different classifications to different distinct population segments of the same vertebrate taxon.

ILLUSTRATIVE CASE OF SPECIES/SUBSPECIES/DPS DEFINITION FOR MARINE MAMMALS

In 2001 NMFS was petitioned to list southern resident killer whales (*Orcinus orca*) as threatened or endangered under the ESA. This group of animals, now numbering around eighty individuals, summers in inland waters near Seattle and Van-

couver. Photographic records collected over the past three decades indicate that these individuals interact exclusively with one another. Genetically and behaviorally, they group with a fish-eating killer whale "form" called "resident" killer whales that range from Washington to at least the Kamchatka Peninsula in Russia. After NMFS concluded that an ESA listing might be warranted for the group called southern residents, the agency conducted a status review using a biological review team composed of government scientists with diverse backgrounds.

In the first round of deliberations, the team determined that southern residents met the criterion for "discreteness" under the joint policy on DPSs. However, the determination of "significance" was far more difficult, largely because of issues surrounding killer whale taxonomy (Krahn et al. 2002). Correctly identifying the killer whale taxon proved critical because the criteria used to evaluate "significance" of a DPS are defined relative to other populations within that taxon. The inability of the team to achieve a consensus on "significance" exposed a number of critical issues involving the treatment of uncertainty in defining the unit to conserve.

In the face of uncertainty, the field of taxonomy is evidentiary as opposed to precautionary, which means that, traditionally, a new species is not named without very strong supportive evidence. In cases where data are poor, the burden of proving taxonomic status falls on the scientist, who must gather the data required to make a strong case for naming a species. In the case of killer whales, the typical requirement of examining a large number of adult skulls could result in taxonomic inaction for decades because skulls can only be obtained from rare strandings of these animals. For some forms of killer whales, skulls may never be obtained. For example, a group of killer whales was photographed killing several sperm whales 50 miles off the central California coast (Pitman et al. 2001). These whales not only did not match any photographic identification catalogs in the North Pacific (which primarily catalog whales found in coastal waters) but also had unique scarring from cookie-cutter sharks. These whales have never been seen again. These animals may represent a pelagic form of killer whales, but skulls may never be found because dead animals will likely sink long before washing up on a beach where they can be collected.

A case is being made for multiple species of killer whales in the Antarctic (Pitman and Ensor 2003). These Antarctic whales look quite different and exhibit different dietary specializations. In the North Pacific, the fish-eating resident form differs genetically from the mammal-eating transient form, despite having overlapping ranges where interbreeding is possible. Although lacking the quantity of data normally required to name species, the biological review team did find that the current designation of one global species for killer whales is probably inaccurate. A similar conclusion was later drawn by a group of specialists convened to address killer whale taxonomy (Reeves et al. 2004): "A straw

poll within the working group indicated little support for the premise that one or more new species could be described on present evidence. Nevertheless, a majority of participants expressed the opinion that more than one species of killer whale exists and will eventually be described and named."

The types of data that are likely to be available in a timely manner are genetic data and morphological data that do not require dead animals (such as photographs of coloration patterns and simple metrics like the shape of the dorsal fin and perhaps lengths when aerial photogrammetry is possible). Under the new definitions noted previously, these data are acceptable for use in describing new species and subspecies and, consequently, faster progress in killer whale taxonomy is expected.

If a unit of animals is recognized as discrete, determining its biological and ecological significance can be confounded by uncertainty regarding the "geographical range" of the species to which it belongs. What is the range of the unperturbed "resident" or "fish-eating form" of killer whale? Uncertainties concerning "range" fall into two main categories: the knowable and the unknowable. The knowable uncertainties pertain to the current range of resident killer whales, which now extends from Puget Sound to the Kamchatka Peninsula, at least in the summer months. The resident form also may be found farther to the west, perhaps ranging to other parts of Russia and Japan, where salmon, thought to be their primary prey, occur. The winter range of residents, including southern residents, remains unknown. These gaps in knowledge can be filled by more extensive sampling (photographic and genetic) and through satellitetagging of known residents.

It is more difficult, if not impossible, to fill knowledge gaps concerning historical distribution. Most marine mammal populations have been greatly reduced in the recent past from various human impacts (overhunting, bycatch, habitat destruction, and prey reduction). Our understanding of distributions of relatively unperturbed populations is poor, and our vision of what is "normal" is very much influenced by distributions observed in only the past few decades. In conservation biology, the redefining of "normal conditions" by each new generation of scientists according to what they observed early in their careers is called the problem of shifting baselines (Pauly 1995, Tegner and Dayton 1997). Southern residents and their prey have both declined in the past few decades, and the possibility that range contraction has already occurred is a plausible one. At present, the primary range of southern residents is Puget Sound-San Juan Islands, but they could have occupied areas that formerly sustained much larger salmon runs, such as waters off Washington, Oregon, and California. Although it may be possible to reconstruct historical range through genetic examination of teeth from museum collections, it is possible that no data are available, and historical range becomes "unknowable." In this case, a "significant portion of the range" can be based on either current range or range inferred from suitable habitat. The problem of "shifting baselines" is pronounced for marine populations where historical distributional data are scarce. It is particularly problematic for species like killer whales, where presence / absence types of data cannot be used because different potential taxa (such as the fish-eating "residents" and the mammal-eating "transients") cannot be readily identified by nonexperts and hence are often referred to as cryptic species.

The final DPS "significance criterion" relates to evidence that the southern residents differ markedly from other populations in genetic characteristics. Although a considerable number of genetic samples have been taken from resident and transient killer whales, interpretation of those samples and the genetic differences between the groups varied widely among scientific experts (Reeves et al. 2004). Thus, killer whales are a particularly good illustrative example of the problem of reducing biological complexity to simple categories for use in a legal framework.

Uncertainty in interpreting genetic data arises because the amount of genetic differentiation that develops between or among demographically isolated groups of animals depends on the numbers of animals in the groups, their social structure, and the length of time these groups tend to remain in existence. Far from providing a tool that allows determination of species status like a litmus test, genetic markers reflect the complex biology of the animals and require scientists to account for that biology when they interpret the genetic data.

Killer whales illustrate the interesting interplay between a species' natural history and its genetic patterns. Apparently, there is a selective advantage for killer whales to become dietary specialists and adapt their social organization accordingly. In the North Pacific, there are at least three types of genetically distinct killer whales. Residents are fish-eaters that specialize in salmon and form relatively large, strictly matrilineal pods (ten to twenty individuals). Both males and females nearly always remain within the pod of their birth, but most mating occurs with individuals from other pods (Barrett-Lennard 2000). Transients are mammal-eaters that are found in much smaller groups. It is unlikely that these groups are strictly matrilineal because it is common to see one or two males alone for long periods. Little is known of the third form, offshores, except that the group size is large and some individuals have been observed eating fish.

Nuclear and mitochondrial DNA data are consistent with little to no current gene flow among these forms, and the magnitude of the differences is quite large (larger than for many acknowledged species). However, interpretation of significance remains difficult. Small populations genetically differentiate more rapidly than large populations through a process called genetic drift, where gene frequencies drift to different levels through the random process of inheritance. Killer whales have low genetic diversity and small populations so the rate of genetic drift is likely to be high.

Further, it is possible that metapopulation dynamics could make founder events likely. Within metapopulations, local populations may go extinct and be recolonized on a relatively frequent basis. When small populations are founded from a larger population, a phenomenon called "lineage sorting" can occur. Imagine that there is a large population that has lived in an ocean basin for many thousands of generations. This population would contain many genetic haplotypes, which are represented by strings of letters for different nucleotide base pairs and are inherited like family names. Some haplotypes are old and differ by many letters from newer haplotypes that differ from one another by only a single letter. If new populations are created from the large old population, there is the possibility that the new ones will contain different frequencies of haplotypes. If these new populations are small and drift such that they end up with only a single name (lineage), then interpretation of the relationship among these new populations can be incorrect without an understanding of the history. For example, if one population ended up with an "old" haplotype and its neighbor ended up with a "new" one, then it might be incorrectly inferred that they had been separated for a time long enough to develop all the letter changes (mutations) between the haplotypes. The correct relationship (that they were recently founded from a large population) can only be reached by considering lineage sorting. However, because we do not know the history, it is also possible that two neighboring populations with very different haplotypes actually have been separated for a very long time. A possible precautionary approach would be to assume that the populations are in fact very different as long as that hypothesis remains plausible.

The southern resident killer whale biological review team was reconvened following the cetacean systematics workshop. After considering the findings of the workshop, most of the scientists agreed not only that more than one species or subspecies was likely under the new definitions, but that North Pacific residents and transients probably belong to separate subspecies (Krahn et al. 2004). Although taxonomic uncertainty remains, the team used a system of likelihood points to vote for different plausible scenarios and ultimately concluded that southern residents did meet the criteria to be defined as a DPS. The National Marine Fisheries Service then announced its intention to list this DPS as threatened under the ESA.

To return to the definition of DPS, the uncertainty associated with interpreting genetic data precludes a litmus test for determining when those data indicate a "marked difference." Instead, a checklist of the type of genetic differences that contribute to evolutionary significance together with guidelines on how to treat uncertainty would prove more beneficial. For example, if fewer than one disperser per generation is consistent with the ability of populations to maintain local adaptations, then a guideline for "marked difference" such as "a 10% chance of fewer than ten dispersers per generation" would allow the incorporation of uncertainty, including factors such as lineage sorting. Of course, putting genetic results in a probabilistic context requires a case-specific modeling approach.

UNITS TO CONSERVE: STOCKS

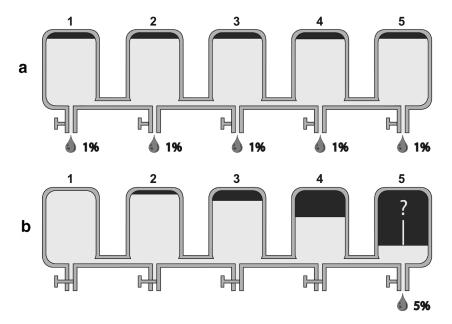
Species, subspecies, and DPSs may contain another level of population structure involving groups of animals that are essentially independent demographically. In other words, the internal dynamics within each group are far more important to the group's maintenance than immigration from neighboring groups. In fact, the degree of exchange or connectivity among such groups is an important determinant of overall population structure and the vulnerability of both the individual groups and the overall metapopulation to human effects. Consider, for example, a case where subsistence hunters from a particular a village want to maintain hunting of harbor seals in perpetuity within a few hours of the village by boat. The immediate concern of the hunters probably would not be preserving the evolutionary legacy of harbor seals, but rather would more likely be making sure that the number of seals they kill is not greater than can be replaced by the combination of local births and seals swimming in from nearby locations.

The connectivity among groups within a larger metapopulation can be symbolized with water bottles linked by unknown levels of flow among the bottles (Fig. 10.2). When the bottles are full, each group has the maximum number of animals that the habitat can support. The water taps indicate drains from groups resulting from human-caused mortality. When the drain rate from each bottle is the same (i.e., where human-caused mortality is proportional to density across the range), it is not necessary to know the bottle structure or the level of flow between the bottles (Fig. 10.2a). This depicts the case where human-caused mortality is proportional to density across the range. In contrast, Figure 10.2b has a heavy drain from only a single bottle in the bottle "range," illustrating cases where incidental kills are restricted to areas near a particular location or human activity. If the objective is to keep all the bottles at a level of at least 50%, then scientists and managers need to know both the "structure" (how many bottles and how much water is in each bottle) and the "connectivity" (i.e., the level of flow among bottles).

Whether management efforts are focused on the overall metapopulation or the demographically independent groups within that population depends on the management objective, which also determines the level of population maintained (10, 50, or 75%). Hence, these demographically independent groups are sometimes called management units. In marine mammal management, they are usually called stocks. Under the U.S. Marine Mammal Protection Act (MMPA), a population stock is a part of a management system that aims to maintain healthy marine ecosystems.

The definitional boundaries between stocks and the next level up at DPSs remain blurred. For example, the "regional populations" of the IUCN (Gärdenfors et al. 2001) are defined both in genetic terms at levels consistent with the DPS concept and at a metapopulation level in terms of "probability of recolonization," which is more consistent with a level

Fig. 10.2. Population structure depicted as a connected system of water bottles with removals from the system shown as drains.



of dispersal typical of stocks. To avoid such confusion, I use stock to mean a unit with a level of demographic independence needed to meet a specific management objective.

The MMPA aims to preserve marine mammal stock structure. The Act specifies that endangered or depleted species "and populations stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population." The Act further states that "the primary objective of their management should be to maintain the health and stability of the marine ecosystem. Whenever consistent with this primary objective, it should be the goal to obtain an optimum and sustainable population keeping in mind the carrying capacity of the habitat." As guidance to interpreting these management objectives, the Act defines "optimum sustainable population" (OSP) with respect to any population stock as "the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element." By regulation, NMFS defined populations to be at OSP when they were between carrying capacity (K) and the maximum net productivity level (MNPL) (Gerrodette and DeMaster 1990). Furthermore, the Act defines "population stock" as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement that interbreed when mature."

Unfortunately, managers have found it problematic to use the criterion "interbreed when mature" for most species. If we interpret the phrase to represent the degree of genetic interchange, then nature presents us with a continuum. Some geographically separate groups of animals may exchange members at the rate of one per generation and others at the rate of 1% per year. If we restrict our definition of a stock to those groups exchanging individuals at the rate of only a few individuals per generation, we will likely have stocks that (1) are distributed over large geographic ranges with disparate habitats, and (2) include multiple groups exhibiting a high degree of demographic independence. Such groups may also exhibit an important degree of ecological independence.

As illustrated in Figure 10.3, improper definition of stocks may undermine management objectives and goals. In the figure, a is the pristine distribution where width represents abundance and length geographic distance. Constrictions in this schematic represent limited movement such that this distribution could be described as a series of population

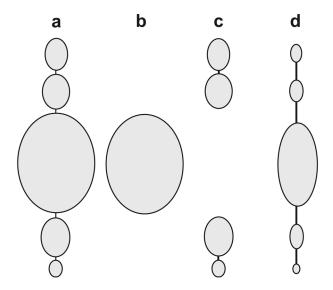


Fig. 10.3. Distribution of pristine populations (a) versus potential distributions after 50% of the total abundance is removed (b–d). Width represents abundance; length represents distance.

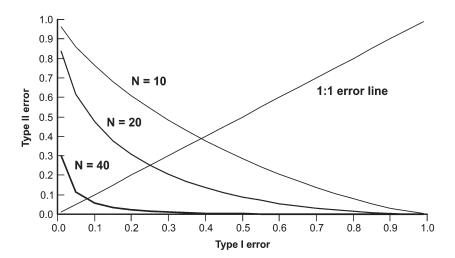


Fig. 10.4. Error trade-off curves for a null hypothesis of panmixia between two populations and an alternate hypothesis of a dispersal rate of 0.75% a year between two populations. The alternate hypothesis is true. Using the typical significance criterion of a Type I error (α) of 0.05, the Type II error would be 0.85, 0.60, and 0.10 for sample sizes (n) of 10, 20, and 40, respectively. Using this criterion means that the scientist is promoting Type II/Type I error ratios of 17 (0.85/0.05), 12 (0.85/0.05), and 2 (0.10/0.05) for the different sample sizes. In other words, when n = 10 the scientist, by using $\alpha = 0.05$, is seventeen times more willing to incorrectly lump populations than to incorrectly split them. Another alternate decision framework is deciding to equalize the Type I and Type II errors, which is shown in the 1:1 error line. Using this decision process would result in using $\alpha = 0.40$ (rather then $\alpha = 0.05$) when n = 10.

stocks connected by dispersal (the aggregate is the metapopulation). Reduction of abundance by 50% could result in any of the other distributions: b, range contraction; c, range fragmentation; or d, range maintenance. Although all may meet the goal of maintaining population stocks within OSP (i.e., about 0.5K), b and c probably do not meet the ecosystem goal. The 1994 amendments to the MMPA allow regulation of human-caused mortality through the calculation of potential biological removals (PBRs) for each affected stock. One element of the equation used to calculate PBR is an estimate of the stock's abundance. However, because there are no "rules" for defining population stocks, any of the above alternatives (i.e., range contraction, fragmentation, or maintenance) could occur depending on the distribution of human-caused mortality. Taylor (1997) developed quantitative methods to determine the dispersal rate (or flow) needed to maintain desired population levels assuming that population stock structure and abundance as well as human-caused mortality are known.

To meet MMPA objectives, the implementing agencies must draw lines on a map to represent stock population boundaries for all forty-eight marine mammal species that occur in U.S. waters. Available data for making such population boundary decisions range from very crude distributional data to very detailed data on movement, morphology, genetics, and distribution. Most of the time, however, the agencies must make their decisions in the face of considerable uncertainty.

A Type I error results from the incorrect splitting of stocks. It is an "overprotection" error and may result in unnecessary restriction of human activities. A Type II error results from the incorrect lumping of stocks. It is an "underprotection" error and may result in a failure to detect a stock falling below MNPL or, worse, its extinction. To calculate the probabilities of making these errors, management objectives must be defined quantitatively.

Methods have been suggested that allow full presentation of the uncertainty in the data without a specific definition

of UTC. For example, Taylor and Dizon (1996) suggested the use of error trade-off curves, which have the important advantage of not forcing the researcher into making a decision as to what error ratio is appropriate for management (Fig. 10.4). Taylor and Dizon (1999) argue that in matters of population structure, policy must precede science because the data can only be properly interpreted once the policy decision concerning the level of population structure that is being sought has been made. Although this is true, use of error trade-off curves at least allows scientists to present results without having to choose an error ratio. However, as seen in Figure 10.4, either a choice has to be made regarding an appropriate dispersal rate or scientists must present a range of possibly relevant dispersal rates, which becomes computationally burdensome.

Participants in a workshop to provide guidelines for implementing the MMPA concluded that stocks must be identified carefully to ensure that the Act's ecosystem goals are met (Wade and Angliss 1997). The stock definition section of this report states:

Many types of information can be used to identify stocks of a species: distribution and movements, population trends, morphological differences, genetic differences, contaminants and natural isotope loads, parasite differences, and oceanographic habitat differences. Evidence of morphological or genetic differences in animals from different geographic regions indicates that these populations are reproductively isolated. Reproductive isolation is proof of demographic isolation, and thus separate management is appropriate when such differences are found. Failure to detect differences experimentally, however, does not mean the opposite. Dispersal rates, though sufficiently high to homogenize morphological or genetic differences detectable experimentally between putative populations may still be insufficient to deliver enough recruits from an unexploited population (source) to an adjacent exploited population (sink) so that the latter remains a functioning element of its ecosystem. Insufficient dispersal between populations where one bears the brunt of exploitation coupled with their inappropriate pooling for management could easily result

in failure to meet MMPA objectives. For example, it is common to have human-caused mortality restricted to a portion of a species' range. Such concentrated mortality (if of a large magnitude) could lead to population fragmentation, a reduction in range, or even the loss of undetected populations, and would only be mitigated by high immigration rates from adjacent areas.

Therefore, careful consideration needs to be given to how stocks are defined. In particular, where mortality is greater than a PBR calculated from the abundance just within the oceanographic region where the human-caused mortality occurs, serious consideration should be given to defining an appropriate management unit in this region. In the absence of adequate information on stock structure and fisheries mortality, a species' range within an ocean should be divided into stocks that represent defensible management units. Examples of such management units include distinct oceanographic regions, semi-isolated habitat areas, and areas of higher density of the species that are separated by relatively lower density areas. Such areas have often been found to represent true biological stocks where sufficient information is available. There is no intent to define stocks that are clearly too small to represent demographically isolated biological populations, but it is noted that for some species genetic and other biological information has confirmed the likely existence of stocks of relatively small spatial scale, such as within Puget Sound, Washington, the Gulf of Maine, or Cook Inlet, Alaska.

In the decade since the PBR scheme was incorporated into the MMPA, relatively few changes have been made to the stock assessment reports regarding stock definition. Some changes have been made using genetic and distributional data as evidence, but accumulation of genetic data has been slow. Even when a respectable sample size has been analyzed, analytical methods remain nonoptimal for defining stocks (see the harbor seal case later in the chapter). As a result, most species within the five regions covered by stock assessment reports are considered to be one single stock. For those single-stock species, underprotection errors are possible, whereas overprotection errors are not.

ILLUSTRATIVE CASE OF STOCK DEFINITION FOR MARINE MAMMALS

Harbor seals can be used to illustrate several points regarding stock definition: (1) analytical methods for defining stocks remain untested and are more likely to underestimate the number of stocks than the converse, and (2) the importance of accurate stock definition is connected to levels of risk of depletion because errors have a graver consequence when risk is high.

The state of analytical methods for detecting and delimiting stock structure is illustrated with an on-going study in Alaska. The decline of harbor seals in some regions of Alaska is a conservation concern because the causes are unknown. In addition, harbor seals are an important subsistence resource for many Alaska Native coastal communities, with an estimated annual take of 2,200–2,800 seals

(Wolf 2001). Management objectives are thus concerned not only with maintaining harbor seals as functioning elements of their ecosystem but also meeting agreed co-management goals to ensure that this species remains a sustainable resource (MMPA as amended 1994, Alaska Native Harbor Seal Commission and National Marine Fisheries Service 2000).

NMFS currently recognizes three separate stocks of harbor seals in Alaska, identified primarily on the basis of regional differences in trends in abundance using data collected prior to 1994 (Small and DeMaster 1995, Hill et al. 1997, Angliss and Lodge 2002). At the time of their designation, however, it was recognized that large gaps existed in our knowledge of dispersal and movement patterns and stock structure, and it was recommended that more information be collected to define more meaningful management units (Small and DeMaster 1995). Over the past decade, a large body of research has been conducted that greatly improves our understanding of harbor seal stock structure, including further trend studies and directed studies of patterns of movement and population genetic structure (summarized in O'Corry-Crowe et al. 2003).

Like many marine mammals, harbor seal distribution is continuous, and samples are obtained opportunistically. Although more than 800 samples have been collected, large sampling gaps remain, and some areas of high density are represented with relatively few samples. This leaves the analyst with two problems: defining hypothetical units to initiate analysis and treating sample gaps.

The analysis of genetic data to identify stocks often employs hypothesis testing, which requires the analyst to stratify the data into initial units (the hypotheses that are being tested). This is problematic for species with continuous distributions.. Martien and Taylor (2003) showed that hypothesis testing to assess stock structure is biased and results in too few stocks when used for species that are continuously distributed with animals at the ends of the range isolated from each other by distance. They showed that the strongest statistical evidence for stock structure was obtained by dividing the range in half, even if the true structure contained many stocks. This resulted from two factors: (1) testing for only two strata directly compared the individuals that differed the most from opposite ends of the range (statistically speaking this comparison has the largest effect size or, in other words, the difference between the hypotheses has the greatest possible magnitude), and (2) each stratum has the largest possible sample size with further subdivision resulting in fewer samples in each stratum (statistical comparisons with the greater sample sizes have greater precision). In addition, even when statistical hypothesis testing indicates the presence of stock structure, it does not provide evidence for the location of the boundary between the stocks.

O'Corry-Crowe et al. (2003) avoided this pitfall by starting with many initial units and using clustering methods to group units that could not be distinguished as demographically independent. These analyses revealed a minimum of twelve demographically isolated units (estimated to have

less than 0.5% dispersal per year among neighboring units). These units were consistent with tagging data that revealed low levels of movement and with trend data that revealed, for example, three different trends even within southeastern Alaska (where three units were proposed based on genetic data that were consistent with the trend data).

In spite of this evidence for more stock structure than previously recognized, data are still insufficient for determining stock boundaries because significant gaps remain in the sampling distribution. For example, it is not clear where the boundary lies between Glacier Bay and the Copper River Delta, which includes Yakutat and Icy Bay. Although Glacier Bay has apparently experienced a strong decline in the past decade and there are local concerns about the status of seals in Yakutat, there are still insufficient samples upon which to base scientific advice concerning stock identity of seals in Yakutat. Thus, despite improvement, management still faces the problem of how to define stocks in the face of uncertainty.

The degree of attention paid to stock definition in different regions has often been commensurate with risks. The large declines in abundance in some parts of Alaska have resulted in the extensive studies just discussed. In contrast, trends in harbor seal abundance are increasing or stable on both coasts of the contiguous United States. There are three stocks defined from Puget Sound south to the California/ Mexico border and only one stock on the U.S. East Coast. Given the scale of harbor seal movements, it is very likely that currently recognized stock structure is too coarse in these areas. Because abundances are currently stable or increasing throughout the range, there is no negative consequence of stock structure errors. There is, however, still some level of risk in the sense that should a sudden decline begin, the agency would have to act with little understanding of stock structure.

CONCLUSIONS

Research needs regarding UTCs are as follows: (1) adequate treatment of uncertainty in taxonomy by application of the precautionary principle and shifting the burden of proof regarding taxon identification, (2) adequate funding to do the science needed to advance marine mammal taxonomy, and (3) development and testing of tools to define UTCs in a probabilistic manner. Managers have to work together with scientists to develop working definitions of UTCs that incorporate scientific uncertainty in a precautionary manner.

Taxonomy

Recent agreements on definitions and criteria for species and subspecies and prioritization for taxonomic research (Tables 10.1, 10.2) should facilitate more rapid advancements in marine mammal taxonomy. Nevertheless, the burden of gathering data still falls on scientists with little to no funding. Thus, although these definitions are improvements, they

still do not explicitly incorporate the treatment of uncertainty and therefore remain biased toward underprotection errors. Progress in taxonomy in the next few years will indicate whether more precautionary definitions and criteria are warranted.

To reduce uncertainty, greater long-term support is needed for research on existing samples and for collection of and research on additional samples from the world's oceans. The needs for current collections are detailed in Reeves et al. (2004) and include integrated database management on a global scale, development of better methods of preservation, and development of better nuclear markers.

Analytical Tool Testing and Development

The scientific challenges with respect to defining UTCs are to gather data that allow UTC definition and to develop analytical methods that minimize errors in UTC definition. Geneticists use a number of methods to analyze their data, but none of these has been tested to see how well they actually detect demographically independent units (stocks). The same can be said for DPSs, although errors are expected to be more minor because the larger degree of genetic differentiation results in higher statistical power to identify DPSs. Methods to analyze genetic data were developed to address evolutionary questions where the levels of genetic differentiation are expected to be strong. An effort is now underway to test how these methods perform using simulated data where the true population structure is known (International Whaling Commission 2004). Scientists also have to develop better methods of integrating disparate types of data in a rigorous fashion. For example, data on distribution, trends in abundance, contaminant levels, morphology, timing of migration or reproductive events, acoustics, telemetry, and genetics all contribute to understanding population structure but relate to that structure on different scales (both spatial and temporal). Perhaps some of these data can contribute to initial hypotheses (or prior distributions in a Bayesian framework) that can be used in model choice exercises.

Ideally, research results should be used to guide conservation decisions. We need more research methods designed specifically for such applied problems. We also have to develop analytical tools that allow researchers to design studies of population structure better; for example, they should be able to say how many samples and how many genetic markers will be needed to provide a given level of certainty about dispersal rates. Scientists interested in detecting trends in abundance have such tools, which allow them to make a preliminary estimate of their ability to detect a given trend with a certain power after a number of surveys. However, in part because the definition of UTC remains nebulous, researchers are presently unable to say how many samples/ markers will be needed to identify UTCs; moreover, after a study, they cannot yet estimate the probability that, given their sample size and distribution, they would have been able to detect multiple stocks that existed in the range of their study.

Incorporating Scientific Uncertainty into Management Definitions of Stock

The management/policy challenge is to phrase policy in a fashion that allows the best use of our knowledge while acknowledging the impact of our ignorance (see Goodman this volume). To better define stocks, our definitions have to incorporate uncertainty both when there are sufficient data and when data are either poor or entirely lacking. A sample rule-of-thumb definition would be "a stock is a population for which the best estimate for the dispersal rate with a neighbor is less than x%/year, where x%/year is considered to be demographically trivial."

A probabilistic definition provides more flexibility. These definitions all have a statement of probability linked to a desired state in a given time period. Such definitions were used in the PBR scheme, which incorporated uncertainty to

proscribe precautionary management (Taylor et al. 2000, Taylor and Wade 2000). Incorporation of uncertainty was accomplished through use of quantitative criteria such as "a 90% chance of a population being greater than 50% of historical numbers in 100 years." The statement of probability results in situations with less certainty receiving more conservative management, which is needed to ensure reaching the desired management state.

ACKNOWLEDGMENTS

This work was funded by the Southwest Fisheries Science Center. Ideas were developed in fruitful discussions within the Protected Resource Division, with special thanks to Andy Dizon, Karen Martien, Susan Chivers, Bill Perrin, Greg [AQ1] O'Corry-Crowe, Rick LeDuc, Paul Wade, and Jay Barlow. The manuscript was improved through reviews by Tim Ragen, Karen Martien, Bill Perrin, and an anonymous reviewer.